Spring 2013

The Effect of Visual Wulst Lesions and Trigeminal Nerve Sectioning on the Discrimination of Magnetic Inclination in the Homing Pigeon (Columba livia)

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The Effect of Visual Wulst Lesions and Trigeminal Nerve Sectioning on the Discrimination of Magnetic Inclination in the Homing Pigeon (*Columba livia*)

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Honors Thesis

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I. Abstract

The ability of homing pigeons to return to their loft from places they have never been to before has fascinated scientists and laymen alike for centuries. As true navigators they both need a map and a compass to be able to find their way. It is well established that homing pigeons, like migratory birds, possess an innate magnetic compass to determine direction. But unlike the type of magnetic compass used by humans, it is an inclination compass that measures the angle between the magnetic field vector and the Earth's surface. Recent work with migratory birds has indicated that the avian magnetic compass is light mediated and appears to be based on a chemical radical-pair mechanism with magnetic information mediated to the brain. This occurs via a visual pathway and is processed in the visual Wulst area of the forebrain called Cluster N. There is, however, also evidence from other avian species that magnetic direction may be detected with iron-based mechanoreceptors in the olfactory epithelium. The goal of this study was to develop a novel conditioning paradigm that required pigeons to solve a spatial task based on magnetic inclination cues to investigate the nature of the pigeon magnetic compass. Our results have shown that the pigeon is clearly able to discriminate inclination values between 0 and 90 degrees. Next, we conducted impairment experiments to identify if pigeons have a light-mediated magnetoreceptor by performing lesions in the visual Wulst area of the forebrain. This allowed us to test whether there is an equivalent area to the Cluster N in this species' forebrain. Our results indicate that this area of the brain is needed. Lastly, we surgically cut the trigeminal nerve to test whether this nerve transmits magnetic inclination cues by way of an iron-based magnetoreceptor. This demonstrates a transmission pathway for magnetic inclination information in pigeons.

Keywords: magnetic compass, inclination, radical-pair mechanism, Cluster N, trigeminal nerve, iron-based magnetoreceptor

II. Introduction

The ability of homing pigeons to return to their loft from distant and unfamiliar places has fascinated scientists for several centuries (Robertson, 2007). They have remained a part of history during some very important times acting as technological advances (Capshew, 1993; Skinner, 1960). The pigeon is a model species to investigate because they can easily adapt to laboratory settings.

As true navigators, homing pigeons need both a map and a compass to successfully fly from point A to point B (Kramer, 1953). A map allows the animal to know where it is in relation to its goal, thus providing positional information. A compass lets the animal translate the position found via the map into a course direction to fly in, thus providing directional information. This tool also helps the animal stay on the path towards point B even when obstacles or anomalies get in the way.

Over the last few decades considerable evidence has accumulated that homing pigeons possess an innate magnetic compass from birth (Wiltschko & Wiltschko, 2007). Later in life, the pigeon learns a second compass known as the sun compass, which is based on the position of the sun in the sky (Able, 2001). Consequently, this leaves using the sun compass at a disadvantage when pigeons are homing under overcast conditions and when the sun does not move at a faster rate in the sky (Santschi, 1911). Therefore, the magnetic compass to plays an important role when navigating (Gould, 1980).

Furthermore, the magnetic compass is based on the detection of inclination cues provided by the Earth's magnetic field (Jungerman, & Rosenblum, 1980). Inclination is the angle between the magnetic field vector and the Earth's surface, with the downward side of the vector pointing to the pole and the upward side point to the equator (Figure 1) (Merrill, & McElhinny, 1983). The Earth's magnetic field involves three axes, the horizontal axis, the vertical axis, and the third dimensional axis, also known as the z-axis (Bloxham, & Gubbins, 1985; Guyodo, & Valet, 1999). Specifically, the measurement of inclination is also known as the deviation from the horizontal axis (Bookman, 1977).

Additionally, research has indicated that the avian magnetic compass is light-mediated and thus dependent on the wavelength of the ambient light. This light-mediated system appears to be based on a chemical radical-pair mechanism in the retina of the eye (Ritz, Adam, & Schulten, 2000). As part of this mechanism, a candidate receptor known as cryptochrome has been identified. Cryptochrome has been shown to switch between a singlet and triplet state depending on orientation of the bird's head in respect to the magnetic field vector (Mouritsen, *et al.,* 2004; Niebner, *et al.,* 2011). Magnetic compass information is then transmitted via the visual pathway, and is processed in the pigeon's forebrain (Heyers, Manns, Luksch, Gunturkun, & Mouritsen, 2007). This is done in an area called "Cluster N" which is located in the visual Wulst section of the forebrain (Mouritsen, Feenders, Liedvogel Wada, & Jarvis, 2005; Zapka, Heyers, Liedvogel, Jarvis, & Mouritsen, 2010).

Recent work with migratory birds and homing pigeons has indicated that the ophthalmic branch of the trigeminal nerve is responsible for transmitting magnetic inclination cues to the brain during navigation (Beason, & Semm, 1996; Heyers, Zapka, Hoffmeister, Wild, & Mouritsen, 2010; Kishkinev, Chernetsov, Heyers, & Mouritsen, 2013; Mora, Davison, Wild, & Walker, 2004). This branch innervates the upper beak of birds and it has been speculated that it may be connecting to the iron-mineral-based magnetoreceptors in the olfactory epithelium (Falkenburg, *et al*., 2010; Kirschvink, & Gould, 1981).

For the homing pigeon, it has been proposed that magnetic direction is either detected with an iron-based magnetoreceptor or that its magnetic compass is light-mediated as in migratory birds (Fleissner, *et al.,* 2003). Additional speculation has proposed that the two systems, iron-based and light-mediated, may be working together in a dual interaction (Mouritsen, & Hore, 2012).

The goal of this project was to develop a conditioning paradigm that required pigeons to solve a spatial orientation task based on magnetic inclination cues. Next, we were interested in determining whether there is an area in the homing pigeon's visual Wulst that is equivalent to the Cluster N identified in migratory birds. For this purpose, we removed the visual Wulst in six homing pigeons and tested whether this treatment would impair the bird's ability to discriminate magnetic inclination cues in the same conditioned spatial orientation task as above. Lastly, we tested whether the ophthalmic branch of the trigeminal nerve is indeed needed to transmit inclination information to the brain. For this reason, we sectioned the trigeminal nerve of five homing pigeons and tested whether this treatment would impair the pigeon's ability to discriminate magnetic inclination cues in the same conditioned spatial orientation task. We also performed sham surgeries on a group of six control homing pigeons in order to determine that the surgical procedure itself has no adverse effects.

III. Materials and Methods

A. Subjects

Nineteen adult homing pigeons (*Columba livia*) were used in the current study. Four of the nineteen homing pigeons were used during the conditioning paradigm. We then used two of the four from this group plus an additional four (of the 19) more homing pigeons for the visual Wulst stage. Finally, an additional 11 (of the 19) homing pigeons were used for the trigeminal nerve stage. The birds were housed at the Bowling Green State University Animal Facility in Bowling Green, Ohio, USA and lived individually in wire mesh cages in a temperature and humidity controlled room on a 12-12 hour light/dark cycle (lights on at 07:00) with *ad libitum* access to grit and water. In order to motivate the birds, they were food deprived to no less than 85% of their baseline weight. This was so they would perform in the magnetic inclination task. This free-feeding weight served as a baseline for weight control. Also, this weight allowed calculation of a critical weight value. This value was held to keep the pigeon from dropping below this weight. If such weight was less than the critical weight, there was a higher chance of the pigeon would not be at an ideal health. If the pigeon was not close to critical weight, and rather, closer to the free-feeding weight, then the animal would not be as motivated to complete given tasks in the arena. All experimental procedures and treatment of birds were approved by Bowling Green State University's Institutional Animal Care and Use Committee.

B. Experimental Setup/Apparatus

A three-axis Ruben coil system was used to stimulate a magnetic field much like that contained in the Earth's core (Figure 2, A.). It was powered by three power supplies; each one a product that generated a homogenous magnetic field inside the center of the coil system. There was a fully automated control panel for the magnetic field inclination inside the coil system with constant background intensity. The intensity remained constant in order to fully interpret all behavior from the pigeons as being an effect from inclination differences.

There was a division of the arena into 4 equal 90° segments. Each segment either stood for a "zero zone" or a "maximum zone". Two of the four segments were assigned as being "zero zones" and the other two segments were assigned as being "maximum zones". This depended on the pseudo-random sequencing during each session.

The "zero zone" was along one axis. It was defined as the point in the arena where inclination was held constant at 0° for the entire 90° segment. This was placed within two of the four zones in the arena. Within the other two zones, the “max zones” were placed. This was where magnetic inclination rapidly increased from 0° at the edge of the “zero zone” to 90° at the mid-point between the two “zero zones”. From this mid-point and continuing in the same direction, the magnetic inclination then rapidly decreased from 90° back down to 0°, where it was again at the starting point of the “zero zone” (Figure 2, B.).

The circular orientation of the arena was located in the center of the magnetic coil system. There was also a central rotatable shaft with a horizontal tracker arm. This was where the walking pigeon was harnessed (Figure 2, C.). An angular decoder detected directional position of the pigeon in the arena over the entire span of time. Computer software tracked the position of the pigeon inside the virtual magnetic map while it simultaneously changed the magnetic field’s inclination. This inclination change that was experienced by the pigeon depended on which zone the pigeon resided in.

Four response-feeder units were located in the four cardinal directions of the orientation arena. Each unit contained a pecking key as well as a feeder magazine (Figure 2, D.). Once the pecking key light was turned on, the pigeon was trained to peck at the key peck button. Since all four of the feeders had this key peck light on, and was turned on at the same time, the pigeon was made to choose between the four of which to peck. When the feeder magazine was made available to the pigeon, it could eat freely for 10 seconds as a reward for choosing the correct direction.

C. Pre-training

During this time, there was an establishment of 85% free-feeding weight to ensure motivation during the conditioning task. The birds were pre-trained as follows. For approximately 5 days, each bird was placed in an experimental harness and fed allowing it to be habituated to the harness while in the home cage and later to be habituated to the magnetic field.

The pigeon was first accustomed to wearing a harness during feeding time each day. This allowed for the pigeon to associate the wearing of the harness with feeding time. Next, the pigeon was attached to the harness by way of the tracker arm in the arena. This is where habituation to the magnetic field occurred. In order to keep positive reinforcement as a part of the training procedure, small piles of food were set up in eight directions on the floor of the arena. This shows the pigeon that the arena was to be seen as a time of feeding.

Afterwards, the pigeon learned to peck the illuminated pecking key. This was done by having first established a relationship between the feeder magazines and food.

Now that the pigeon is used to eat from the trays of food, the key peck lights were incorporated by using Oreo cream which attached a pellet of food to the key peck button. This middle step was used to bridge the gap between adjusting eating from the feeders and going to the key pecking light for food from the feeders to be raised. It was encouraged to peck multiple times at the key peck light before the feeder comes up once the bird began to repeatedly eat the pellet off of the key peck light.

The pigeon developed the ability to peck the key peck lights after the light had been illuminated. Also, the Oreo cream incentive and pellet of food from the key peck buttons was removed. As the pigeon learned to peck the key peck light multiple times, only after it has been illuminated, it understood that food is raised only after pecking this area of the feeder magazine.

Throughout the later stages of pre-training, each location was reinforced by food given to the pigeon after the first four choices at any of the four given directions. This was done to avoid bias for any one feeder and ultimately, any one direction.

D. Conditioned Choice Training

The location of the "max zones" at either the East and West feeders or the North and South feeders was alternated in a pseudo-random ordering for each of the 32 trials per session. Correspondingly, the "zero zones" were at either the North and South feeders or the East and West feeders respectively, whichever the "max zones" were not at.

The sampling phase consisted of the pigeon walking on the tracker arm for 15 seconds. Once the 15 seconds were up, all 4 of the feeder response units were illuminated. This was known as the choice phase. The correct choice, being either of two feeders that were located in the "max zones" during that trial, was rewarded by raising the feeder magazines and displaying the pigeon with food. The incorrect choice, being either of two feeders located in the "zero zones" during that trial, resulted in a time penalty of 15 seconds that was added to ITI. This is the inter-trial interval which was 5 seconds. If the pigeon choose wrong, then the ITI would be increased to 20 seconds, being that of the original 5 seconds and an additional 15 seconds. If the pigeon choose incorrectly, then the same stimulus was repeated until the correct choice was made. This part of the procedure only occurred during the correction trials.

E. Conditioned Choice Testing

After 3 to 5 sessions with correction trials were conducted, baseline testing began with daily sessions. During this time, the percentage was calculated by the number of correct choices made by the pigeon. This was recorded as data.

F. Visual Wulst Lesions

After baseline testing, all pigeons were prepared for surgery. This included a period of at least 12 hours on *ad libitum* access to food and water. The night before surgeries, all pigeons had their food taken away. On the day of surgery, each pigeon went under general anesthesia and the visual Wulst in the homing pigeon's forebrain (N = 7) was aspirated based on the general stereotaxic guidelines structural delineations from Kraten & Hodos' (1967) stereotaxic atlas of the pigeon brain. Following surgery, a recovery period of two weeks was maintained while all pigeons were put on *ad libitum* access to food and water. All pigeons were then put on food restriction where post-lesion data collection began.

G. Trigeminal Nerve Sectioning

After baseline testing, all pigeons were prepared for surgery. This included a period of at least 12 hours on *ad libitum* access to food and water. The night before surgeries, all pigeons had their food taken away. One the day of surgery, each pigeon went under general anesthesia and was then split into two groups: a group of experimental birds (N = 5) and a group of control birds (N = 6). The experimental birds underwent all steps of surgery where the trigeminal nerve near the pigeon's upper beak was sectioned in the orbital socket. The control birds went through all of the same steps as the experimental birds, except the trigeminal nerve was only touched and not sectioned. Following surgery, a recovery period of two weeks was maintained while all pigeons were put on *ad libitum* access to food and water. All pigeons were then put on food restriction where post-operative data collection began.

H. Visual Wulst Lesion Histology and Reconstruction

After the animals completed testing, the visual Wulst-lesioned birds were sacrificed to determine the extent of lesion damage. The birds received a lethal injection of a pentobarbital based euthanasia solution (100mg/kg i.p) and perfused intracardially with approximately 250 mL of 0.9% saline followed by 4% paraformaldehyde. The brains were then harvested and placed into 4% paraformaldehyde for 24 hours after which they were transferred to 30% sucrose solution for 48-96 hours for cryoprotection. Brains were sectioned at 40 µm on a freezing microtome, with every fourth section mounted on a gel coated slide. Tissue was differentiated with cresyl violet stain. Lesions were reconstructed and quantitatively analyzed using Stereo Investigator image analysis software (MicroBrightField, Inc.). The percent of total septal damage was calculated for each bird.

IV. Results

A. Lesion Damage

Figure 3 summarizes the damage to the visual Wulst area and surrounding regions in the lesioned birds. Although some variability in lesion damage was found among subjects, most birds sustained substantial damage to the visual Wulst area. In some pigeons,damage extended beyond the visual Wulst area. Visual inspection of visual Wulst damage in a few birds suggested differences between the hemispheres.

B. Behavior

For the first stage of testing, our results for the conditioning paradigm show each homing pigeon’s daily performance as well as an average performance per day, including all four pigeons. This was based off of established learning curves and experimental data (Figure 4, A.). Also, data collection occurred when the magnetic field was turned off during, namely, control sessions. This was based off of experimental data collected for each bird and a calculated average for all birds (Figure 4, B.).

For the second stage of testing, our results for the visual Wulst lesions show each bird’s - performance as well as an average for all birds’ performances when the visual Wulst area of the forebrain is impaired. This was based off of data collection during both pre-lesion testing (baseline) and post-lesion testing (Figure 5).

For the third stage of testing, out results for the trigeminal nerve lesions show an overall mean of the birds in both the experimental group and the control group. This was based off of data collection during both pre-surgery (baseline) and post-surgery testing (Figure 6).

V. Discussion

For the conditioning paradigm series, data collection as well as post-collection analysis allowed us to come to the conclusion that the homing pigeon can be conditioned to solve a spatial task based on magnetic inclination cues. Also, further indication that the pigeons are conditioned to the inclination cues and not an external sensory cue was provided when the magnetic field was turned off during control sessions. This was displayed by the birds making significantly more correct choices to the reinforced feeder when the magnetic field was on, as compared to when the field was turned off. Moreover, when the field was on, and magnetic inclination information was available, the birds chose correctly significantly more than chance performance across multiple sessions throughout testing. The pigeons were able to discriminate between the feeders associated with inclinations of 0° to 90°.

During pre-lesion (baseline) sessions of the visual Wulst series, the pigeons were able to learn to discriminate between the feeders associated with either 0 degree inclination or 90 degree inclination with performances consistently and clearly residing above chance level (50%). After removal of the visual Wulst region of the pigeon's forebrain, discrimination performance dropped to around chance level in all pigeons with the percentage of correct choices ranging mostly with 5% above or below chance level.

Our results provide the first evidence that the visual Wulst region of homing pigeons, as previously found with migratory birds, is involved in the processing of inclination information. How this information is used to determine compass direction remains still needs to be investigated further in both pigeons and migratory birds. Data collection in this project is still ongoing and a control series involving the discrimination of visual cues in the same experimental setup will shortly be conducted with these birds to ensure that the experimental treatment did not have general effects on the birds' cognitive abilities to perform discrimination tasks.

During pre-surgery (baseline) sessions of the trigeminal nerve series, the pigeons were able to learn to discriminate between the feeders associated with either 0 degree inclination or 90 degree inclination change with performances consistently and clearly residing above chance level (50%). After sectioning of the trigeminal nerve, discrimination performance dropped to around chance level in pigeons in the cut group with the percentage of correct choices ranging mostly with 5% above or below chance level. The pigeons in the control group were able to discriminate the inclination information of the magnetic field after sham surgeries for sessions eight through 15. Thereafter, performance of the control birds declined and required re-training of all birds. Data collection since re-training is still ongoing.

Our results provide the first evidence that the ophthalmic branch of the trigeminal nerve of homing pigeons, as previously found with migratory birds, appears to be involved in the transmission of inclination information. How this information is used to determine compass direction still needs to be investigated further in both pigeons and migratory birds. Data collection in this project is still ongoing and a control series involving the discrimination of visual cues in the same experimental setup will shortly be conducted with these birds to ensure that the experimental treatment did not have general effects on the birds' cognitive abilities to perform discrimination tasks.

Similarly since in all three series, the literature further supports the notion that migrating species take use of the magnetic sense to navigate. This discovery of an inclination paradigm, as well as navigational mechanisms in both the visual Wulst and the trigeminal nerve, now illustrated in domesticated birds shows an expansion of species who take use of inclination while navigating. Our study has broadened this area of research because our task involves operant conditioning, whereas past studies on migratory birds have only described automatic, innate behaviors.

It is not clear whether the birds used the absolute values or the rate of change in inclination to make this distinction. Even though the existence of an avian inclination compass has been well documented since the 1970s, this is the first time homing pigeons, or any bird species for that matter, have been conditioned to detect inclination changes, despite several previous attempts. We therefore now have a novel behavioral paradigm that is well suited for further anatomical, neurophysiological, and psychophysical analysis of the avian magnetic compass. We will follow up this project with more impairment studies to test whether the hippocampus area in homing pigeons is involved in spatial navigation.

As stated previously, it has been suggested that for migratory birds, a light-mediated magnetic compass or an iron-based magnetoreceptor is key to their navigational abilities. We still think it is possible that birds may be using a mixture of both mechanisms when navigating. Furthermore, we will conduct immediate early gene studies with ZENK that will take place in an area in the Visual Wulst of the pigeon's forebrain that is analogous to the Cluster N region. This Cluster N region has already been identified in migratory birds. This will lead to a determination in the specific region responsible for processing magnetic compass information. Finally, we will expand this technique into a virtual magnetic map approach, as we have already done for magnetic intensity cues.

VI. Conclusion

Based on the magnetic inclination cues given, a conditioning paradigm was successfully found that required the pigeons to solve a spatial orientation task in relation to its magnetic field.

This paradigm then permitted us to investigate for the first time the sensory mechanisms underlying the magnetic compass in the laboratory.

During our visual Wulst series, baseline performance level was recorded for each bird over a series of seven sessions. Next, the visual Wulst area of the pigeon's forebrain was removed in each bird as this region had been implicated in the processing of magnetic compass cues in migratory birds, which like homing pigeons, possess a magnetic compass. Ten post-operative data collecting sessions were conducted to measure any effect that came from the lesion treatment. Following lesions, average discrimination performances dropped to 50% chance level, indicating that this area of the brain is needed to process the magnetic field of the Earth.

The conditioning paradigm also permitted us to investigate the possible role of the trigeminal nerve in the magnetic compass in the laboratory. Baseline performance level was recorded for each bird over a series of ten sessions. Next, the trigeminal nerve near the pigeon's upper beak (this region had been implicated in the transmission of magnetic compass cues in migratory birds, which like homing pigeons possess a magnetic compass) was sectioned in five birds. Six birds were placed in a control group and underwent sham surgery to test for any adverse effects due to surgery.

Thirty post-operative data collecting sessions were conducted to determine whether the pigeons were still able to perform the magnetic inclination discrimination task. Following sectioning, average discrimination performances for the group of cut birds dropped to 50% chance level, where average discrimination performances for the group of control birds remained above 50% chance level for at least some sessions. This indicates that this area of the trigeminal nerve may be needed to process the magnetic field of the Earth.

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VIII. Figure Captions

Figure 1. Magnetic field vectors (black arrows) for different latitudes on Earth. Note that the inclination angle changes with latitude increasing towards the poles.

Figure 2. A. Traditional arena approach with a power source to control the magnetic field. B. A diagram of the magnetic field acting on the arena with no change versus rapid inclination change. The two feeders in each picture show the max-max zones. This is where the bird is rewarded. C. The pigeon is accustomed to wearing the harness and then to being attached in the harness to the tracker arm. D. The pigeon walking on the tracker arm for 15 seconds. This completes the sampling phase. After the 15 seconds are up, the pecking keys on all four of the feeder-response units are illuminated. This begins the choice phase.

Figure 3. Schematic coronal sections of the visual Wulst lesion reconstructions at 1.0 mm intervals from anterior (A 14.5) to posterior (A 9.5) according to the atlas of Karten and Hodos (1967), labeled according to the revised nomenclature (Reiner et al., 2004). Black areas identify damage in at least 5 of 7 pigeons, and gray areas identify damage in at least 3 pigeons. Abbreviations: APH, area parahippocampus; HA, hyperpallium accessorium; HD, hyperpallium dorsale; M, mesopallium.

Figure 4. A. Percentage correct choices per session for individual birds and averaged across all three birds. Chance level (50%) is indicated by the black horizontal line. B. Percentage correct choices for the standard and the control sessions. Standard sessions consisted of 32 “Coil On” trials. The control sessions consisted of 16 “Coil On” trials and 16 “Coil Off” trials presented on a pseudorandom schedule. The second half of control sessions consisted of 32 “Coil Off” trials.

Figure 5. Percentage of correct choices per session for individual pigeons and averaged across birds. Chance level (50%) is indicated by black horizontal line. Pre-operative sessions are indicated by being on the left hand side of the vertical dashed line. Post-operative sessions are indicated by being on the right hand side of the vertical dashed line.

Figure 6. Percentage of correct choices per session for individual pigeons and averaged across five sectioned and six control birds. Chance level (50%) is indicated by black horizontal line. Vertical dashed line indicates time of surgery. Re-training sessions occurred during sessions 21 – 27.

Figure 1

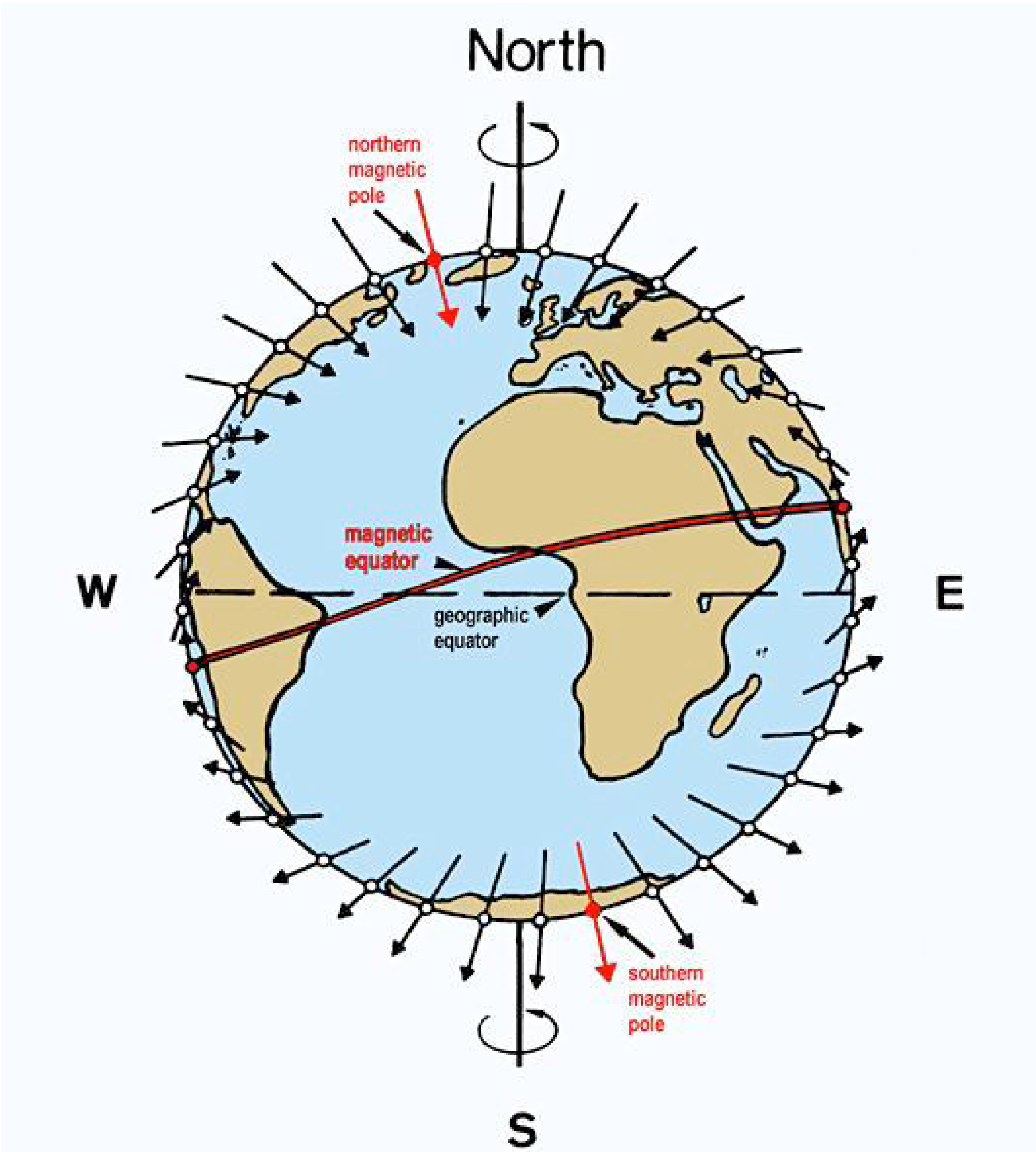

North
northern
magnetic
pole
magnetic
equator
W
geographic
equator
E
southern
magnetic
pole
S

Figure 2

A. Arena

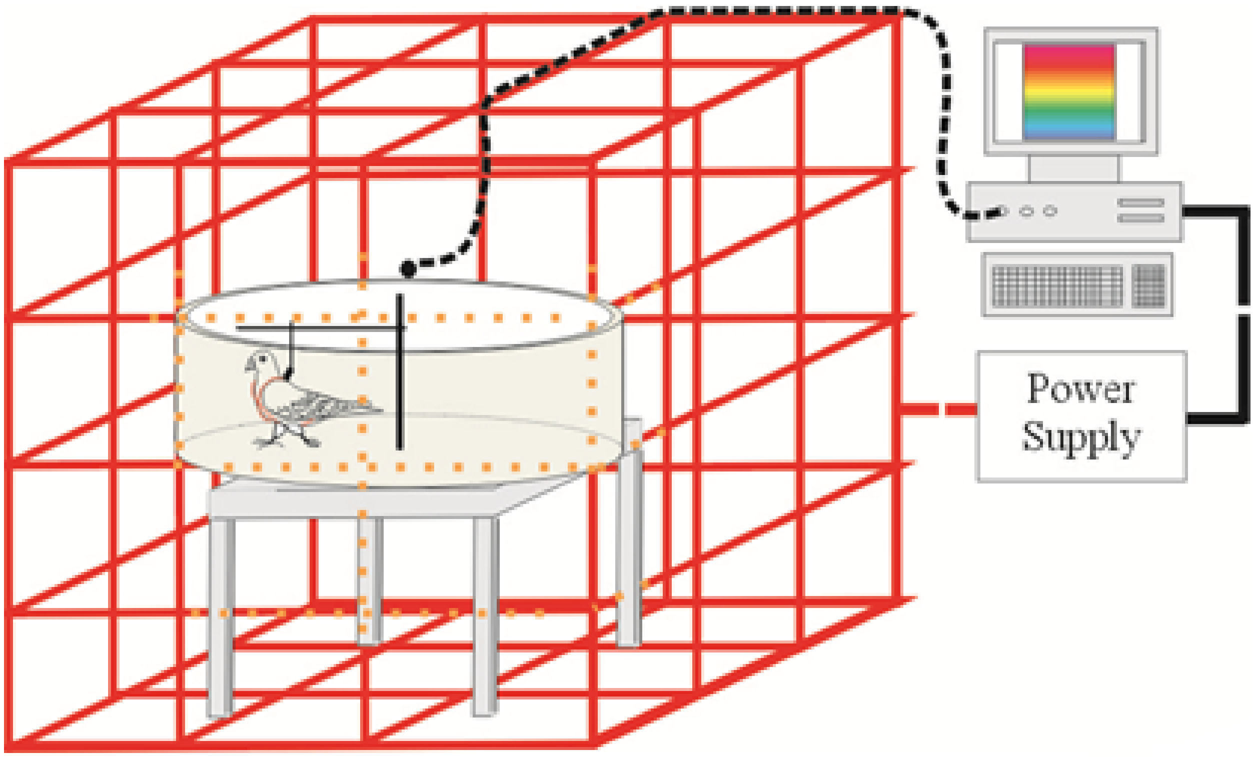
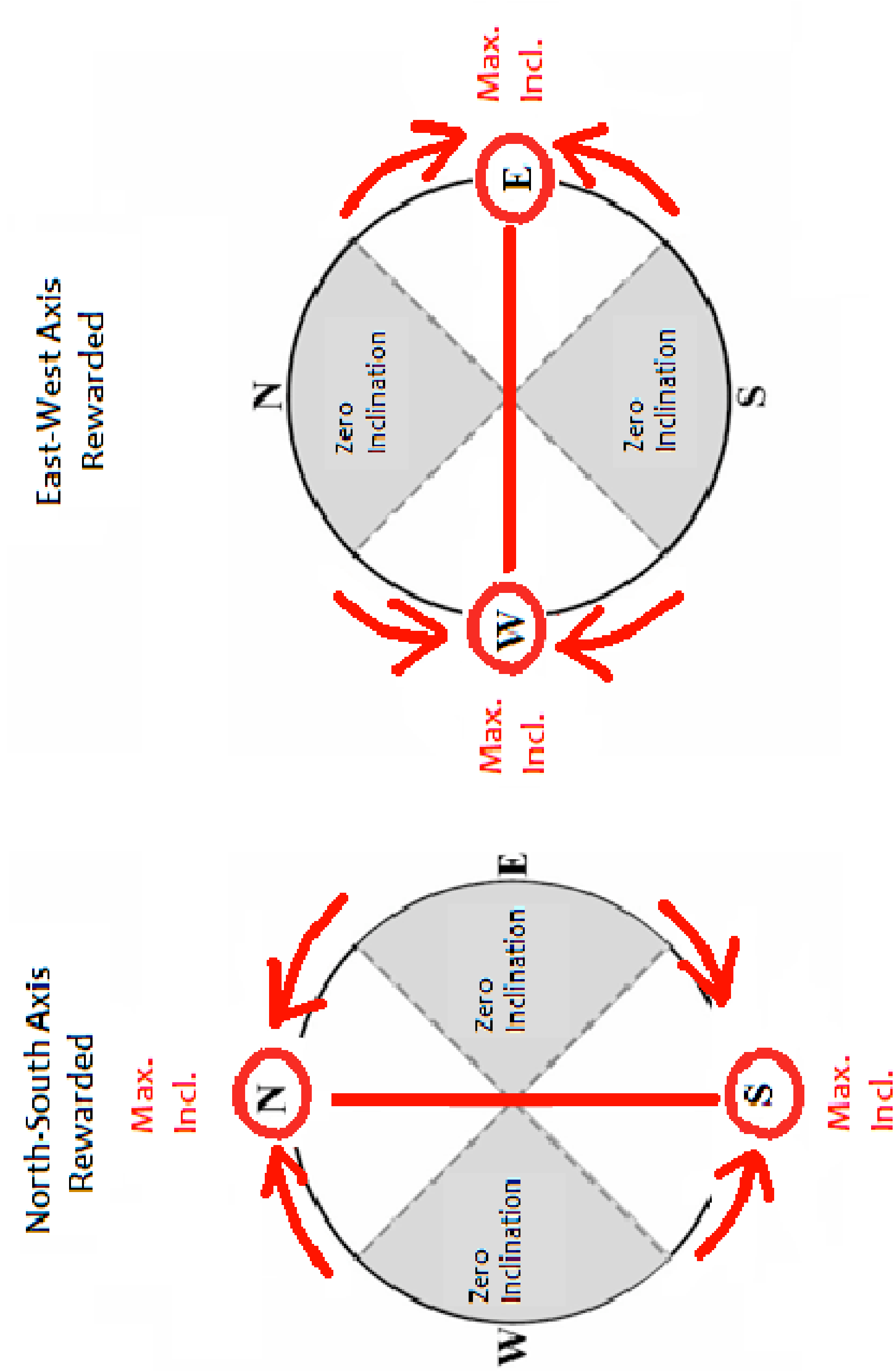
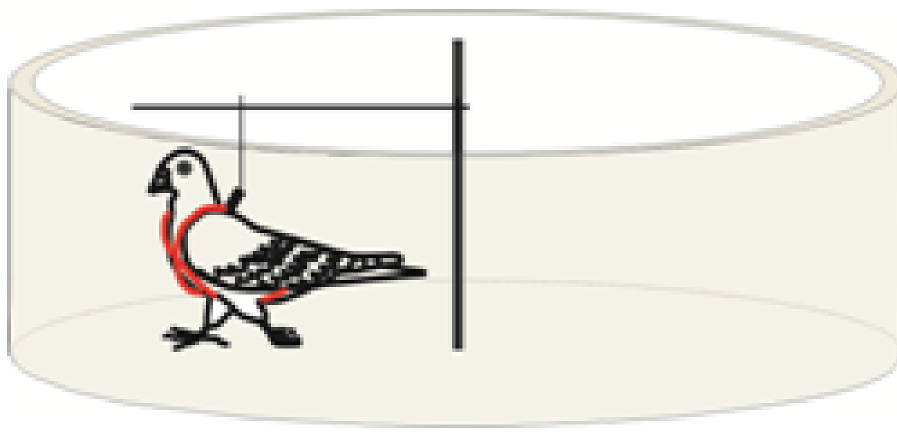


Figure 2

B. Magnetic Field



C. Harness/Tracker Arm



D. Feeder-Response Units

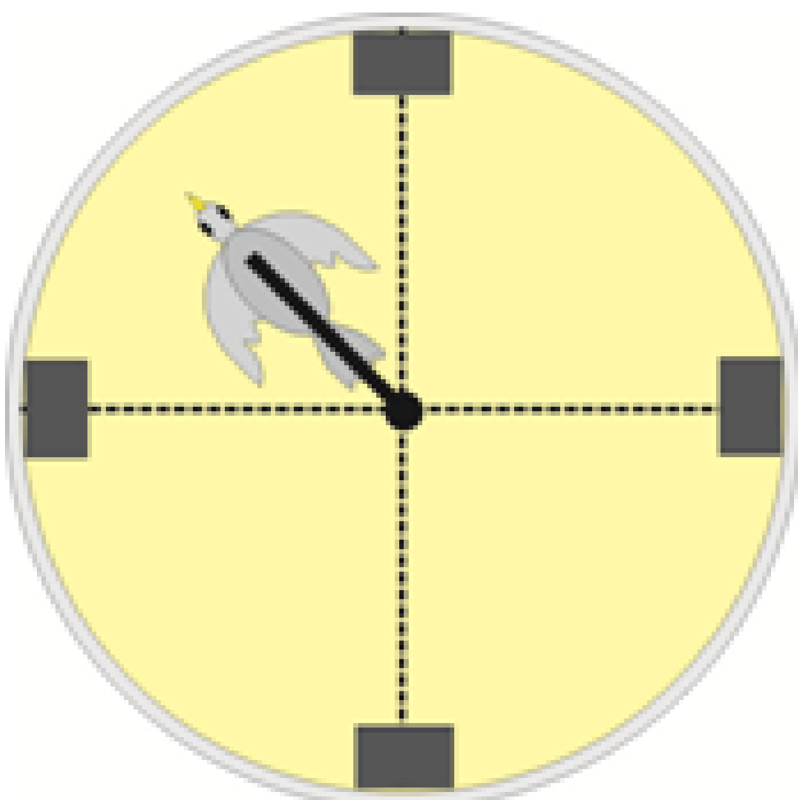


Figure 3

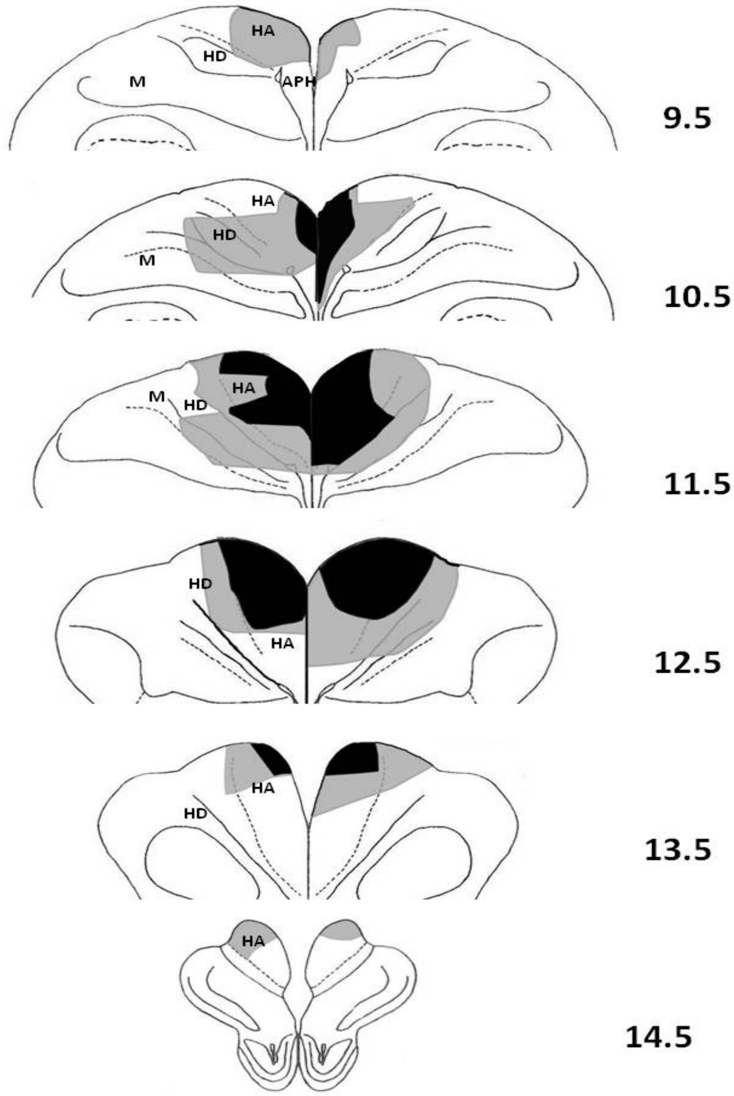


Figure 4

A. Conditioning Paradigm Graph

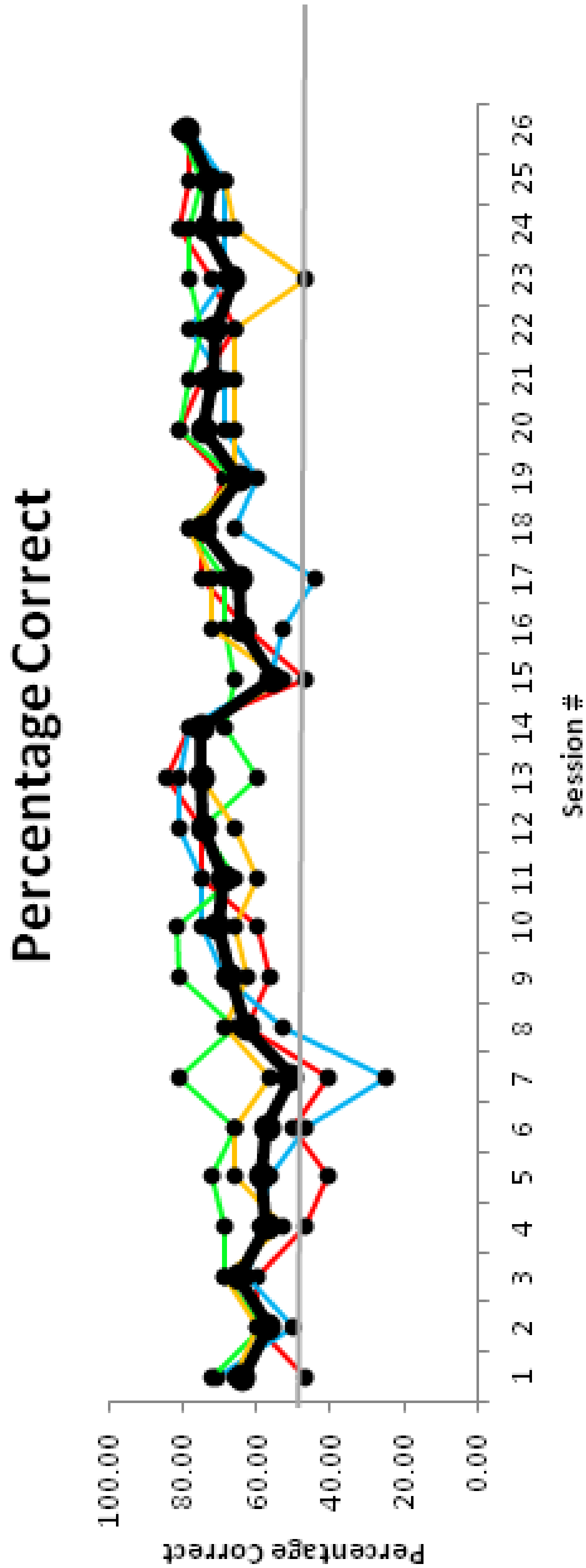


Figure 4

B. Coils Off Control Graph

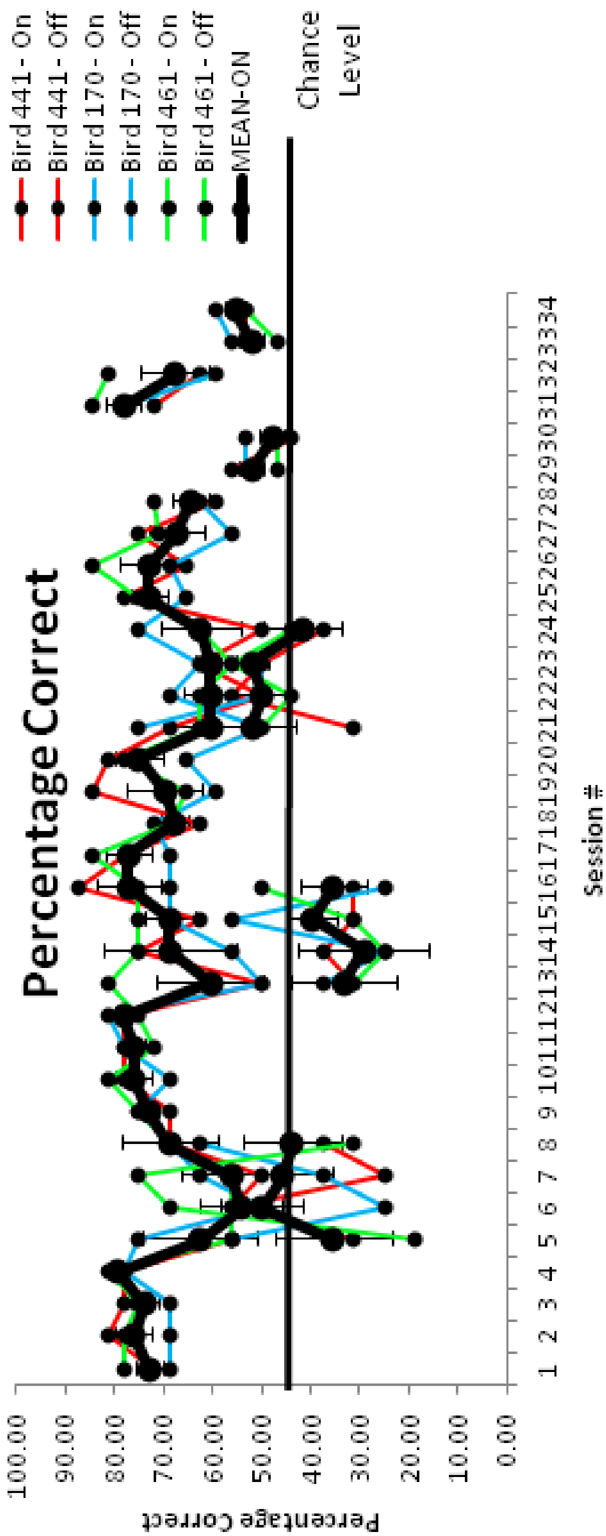


Figure 5

Visual Wulst Lesion Graph

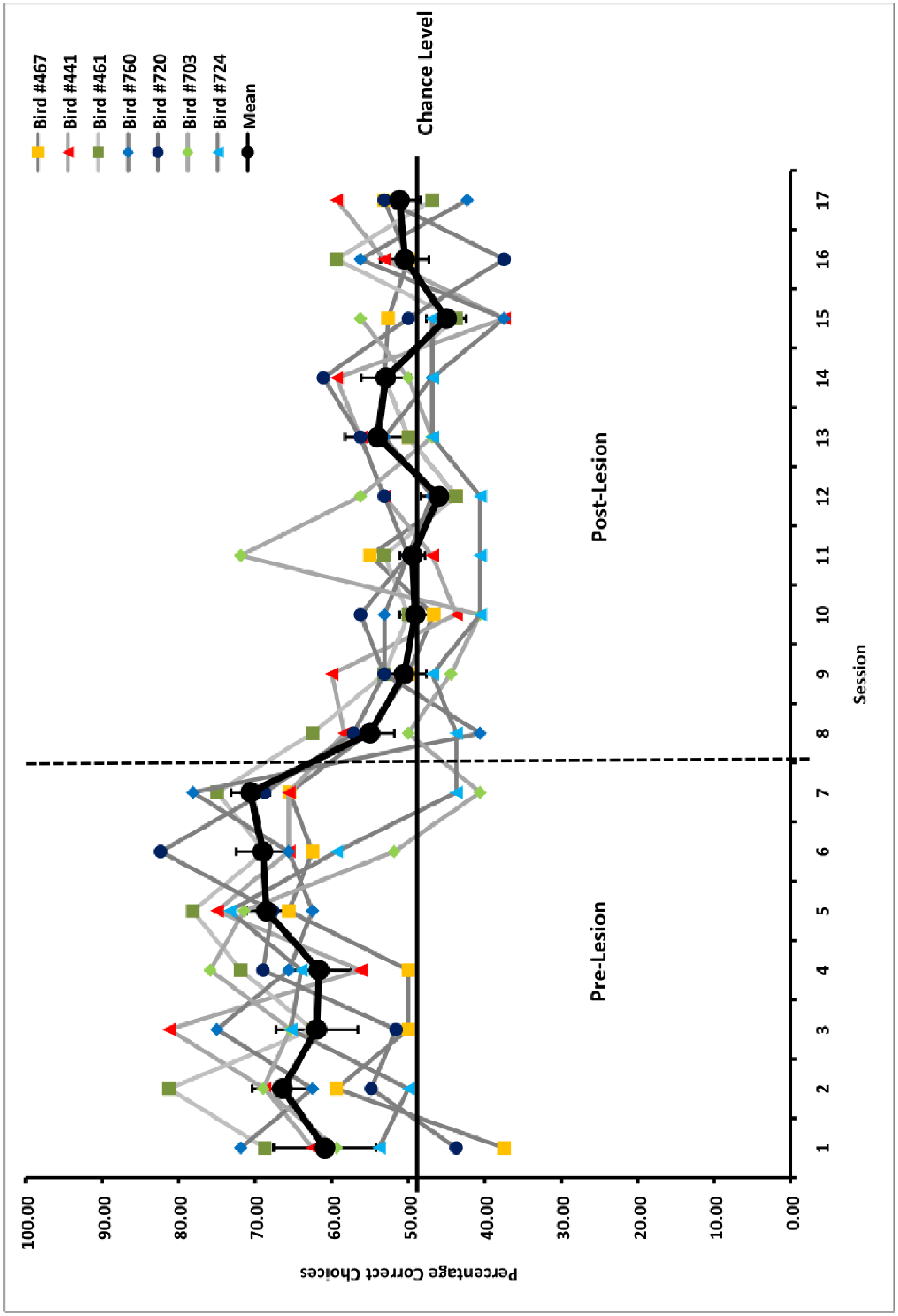


Figure 6

Trigeminal Nerve Sectioning Graph